



South American Opisthobranchia (*Mollusca: Gastropoda*) collected by Charles Darwin during the "Beagle" expedition in 1832-1835

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ABSTRACT

CHARLES DARWIN collected a number of opisthobranch molluscs from Magellanic waters and briefly described them within the "Zoology Notes", a collection of hand-written field notes. None of these species, roughly called "Doris", "Cavolina", "nudibranch", or "Pleurobranchus", were either identified or named by DARWIN; museum material could not be traced. However, my recent, comprehensive taxonomic review of Chilean opisthobranchs paired with Prof. KEYNES' (Cambridge) first public edition of the Zoology Notes now provide the faunistic and descriptive background needed to interpret DARWIN's notes. While some descriptions are very rudimentary, others give surprisingly detailed morphological and biological information. The present study identifies five of DARWIN's Magellanic opisthobranchs to species level, i.e. the pleurobranchid *Berbella platei* Bergh, 1898, the common aeolid *Phidiana lottini* (Lesson, 1831) and the doridoidean nudibranchs *Anisodoris fontaini* (d'Orbigny, 1837), and *Anisodoris punctulata* (d'Orbigny, 1837). *Thecacera darwini* Pruvot-Fol, 1950, a species which was named in honour of a southern Chilean polycerid collected by DARWIN is confirmed to really refer to the "nudibranch coming nearest to Scyllaea" from Cerro Tres Montes which was described accurately by DARWIN more than a century before.

RIASSUNTO

CHARLES DARWIN raccolse un certo numero di molluschi opistobranchi nell'area magellanica, descrivendoli nelle "Zoology Notes", una raccolta manoscritta di osservazioni di campo. Nove di queste specie, grossolanamente chiamate "Doris", "Cavolina", "nudibranch" o "Pleurobranchus", non furono mai descritte dallo stesso DARWIN nè è stato possibile rintracciarle in collezioni museali. Le recenti review sui molluschi opistobranchi del Cile e la recente pubblicazione delle "Zoology Notes" a cura del Prof. R.D. KEYNES (Cambridge) hanno permesso di interpretare le osservazioni di DARWIN. Mentre alcune note sono molto superficiali, altre danno dettagliate informazioni sia morfologiche che biologiche. Il presente studio permette di identificare, a livello specifico, 5 specie osservate da DARWIN nell'area magellanica: *Berbella platei* Bergh, 1898, il comune colide *Phidiana lottini* (Lesson, 1831) e i doredacei *Anisodoris fontaini* (d'Orbigny, 1837) e *Anisodoris punctulata* (d'Orbigny, 1837). Viene infine confermato che *Thecacera darwini* Pruvot-Fol, 1950 è realmente riferibile a "nudibranch coming nearest to Scyllaea", un policeride raccolto e descritto con accuratezza da DARWIN più di cent'anni prima della descrizione originale.

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INTRODUCTION

During the famous "Beagle" Cruise, DARWIN collected an enormous variety of marine organisms. He documented his findings within the "Zoology Notes", a collection of hand-written field notes. The first public version of the "Zoology Notes" edited and commented on by Prof. KEYNES (in press) presents live descriptions of several opisthobranch molluscs from South America: one polycerid doridoidean which was mentioned as "Nudibranch allied to Scyllaea?", one aeolid "Cavolina" and some "Aplysia" from Brazil, but most species were collected from Magellanic waters, i.e. from the Falkland Islands, Tierra del Fuego and Chiloé Island, southern Chile. None of these species, roughly called "Doris", "Cavolina" "nudibranch" or "Pleurobranchus", was identified or named by DARWIN. At that time only two nudibranch species were known from temperate waters of South America: the doridoidean *Doris amarilla* Pöppig, 1829, which was not adequately described for reidentification (SCHRÖDL, 1996), and the aeolidoidean *Phidiana lottini* (Lesson, 1831) which recently (see SCHRÖDL, 1996, 1997b) was considered to be a senior

synonym of the well-known *Phidiana inca* (d'Orbigny, 1837). More significant faunistic contributions were published later, i.e. those of D'ORBIGNY (1835-1846; "Voyage dans l'Amerique Méridionale"), GOULD (1852, 1856; "United States Exploring Expedition"), ABRAHAM (1877), and ROCHEBRUNE & MABILLE (1891; "Mission Scientifique du Cap Horn"), however, all just provided external, sometimes very sketchy descriptions. Later workers such as BERGH (1884, 1894, 1898), ELIOT (1907), ODHNER (1926), MARCUS (1959), and MARCUS & MARCUS (1969) added anatomical data on many species but sparse information on living specimens. Just recently, external descriptions of living Chilean opisthobranchs and detailed taxonomic revisions (e.g. SCHRÖDL, 1996, 1997a,c, 1999, 2000a,b), paired with Prof. KEYNES' edition of the Zoology Notes (KEYNES, in press), allow to interpret DARWIN's notes.

MATERIAL AND METHODS

Text in quotation marks refers to DARWIN's (CD) original notes which were taken from Prof. KEYNES' edition of the

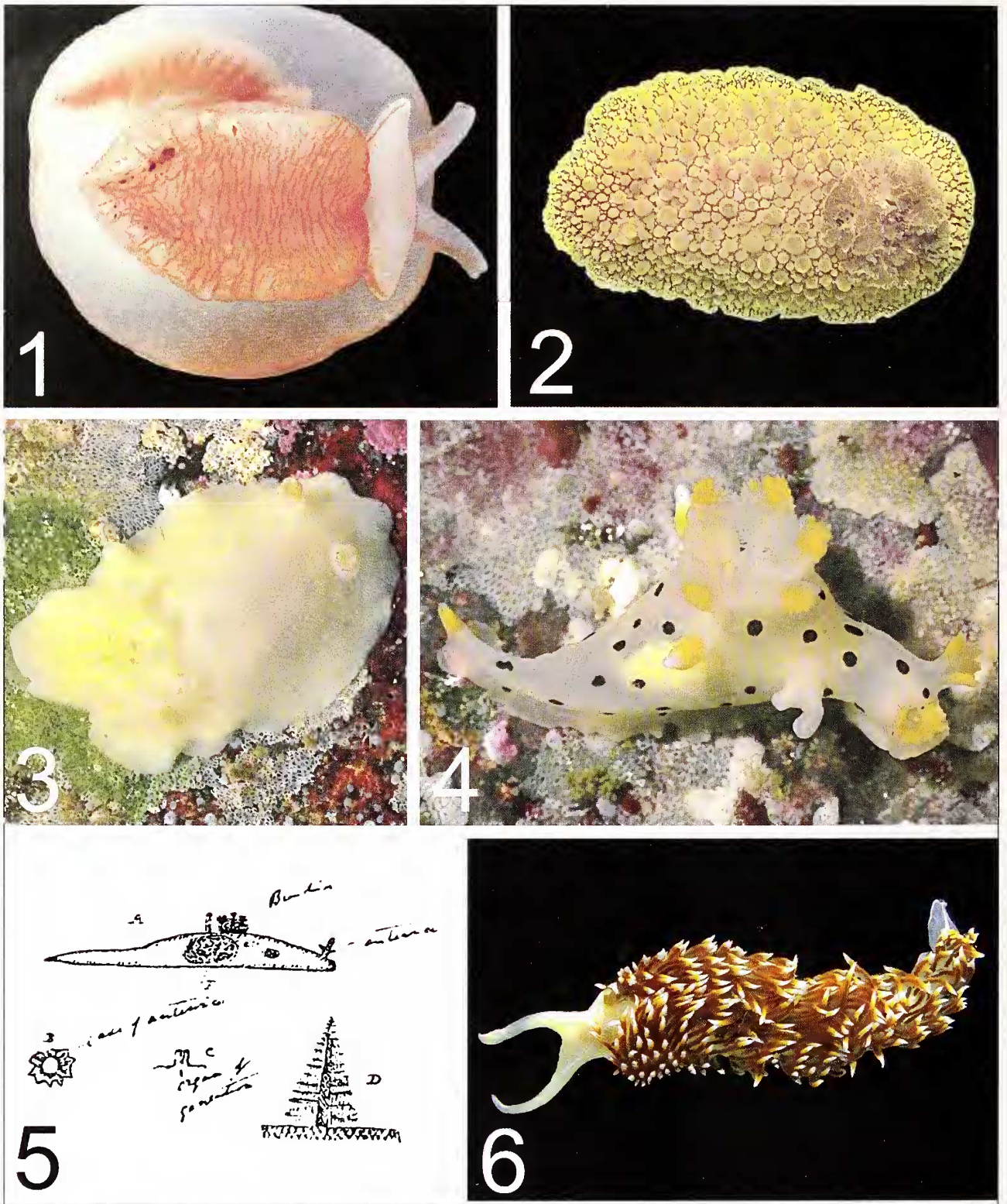


Figure 1: *Berthella platei*, living specimen (30 mm) from Lenca, ventral view.

Figure 2: *Anisodoris fontaini*, living specimen (55 mm) from the Bahía de Coliumo

Figure 3: *Anisodoris punctuolata*, living specimen (40 mm) from the Bahía de Coliumo (from SCHRÖDL, 1996: pl. III, fig. 20).

Figure 4: *Thecacera darwini*, living specimen (25 mm) from the Bahía de Coliumo (from SCHRÖDL, 1996: pl. V, fig. 33).

Figure 5: *Thecacera darwini*, DARWIN'S original illustration (pl. 16, fig. 1; from KEYNES, in press, modified). Note the whole specimen in lateral view ("A"), the rhinophoral sheaths in view from above ("B"), a schematic drawing of the everted genital ducts ("C"), and a sketchy drawing of a single gill ("D").

Figure 6: *Phidiana lottini*, living specimen (60 mm) from the Bahía de Coliumo (from SCHRÖDL, 1996: pl. VII, fig. 41).



“Zoology Notes” (KEYNES, in press). Text in parenthesis within these citations are comments of the author. Some museum material of opisthobranchs collected during the “Beagle” was traced in the Cambridge University Museum of Zoology: only an *Aplysia* specimen and a specimen of *Bulla nitidula* from St. Jago, Cape Verde Islands are still in the collection (PREECE, pers. com.)

SYSTEMATICS

Incertae sedis

“Gasteroapterus”, “Port Famine” (Puerto Hambre, Magellan Strait), June 1834, roots of kelp, CD Page 264, species No. 996.

Remarks: The “straw-yellow” specimen was briefly described by DARWIN as having a mantle with sinuous edge and far surpassing the foot (mantle length 3.8 cm, width 2.8 cm). “Inferior antennae connected for 3/4 of length by a membrane” may either refer to a cephalaspidean head shield with projecting corners, or, more likely, to a pleurobranch oral veil with projecting oral tentacles. “Superior antennae” are “slightly winged”, “branchiae” and viscera are “of rather a dark tint”. No shell was mentioned. If truly a member of the genus *Gastropteron* Kosse, 1813, this would be the first and only record of Gastropteridae from temperate South American waters. However, the presence of two pairs of “antennae” makes this identification doubtful. On the other hand, no pleurobranch (or any other shell-less opisthobranch species with a mantle being much wider than the foot) with a sinuous mantle edge is known from the Magellanic region so far.

Notaspidea

Pleurobranchidae Fèrrusac, 1828

Genus *Bertbella* Blainville, 1825

Bertbella platei (Bergh, 1898).

(Figure 1)

“Pleurobranchus (crossed out) Sigaretus”, east end of Beagle Channel, February 1834, at 3 m depth, roots of “Fucus Giganticus” (giant kelp), CD Page 217, Species No. 861.

REMARKS

DARWIN’s description alone does not allow a more detailed identification other than the family Pleurobranchidae. However, according to a recent revision (SCHRÖDL, 1999) there is only one pleurobranchid species known from the Pacific part of the Magellanic region and from the southern Patagonian shelf, *Bertbella platei* (Bergh, 1898). Therefore, it is highly probable that DARWIN first examined *B. platei*, 60 years before L. PLATE collected this species and gave it to BERGH (1898) for species description. Characterizing the invertebrate fauna around Chiloé Island in general terms, DARWIN (page 242) mentioned “Pleurobranchus” to be common.

Nudibranchia

Doridoidea

Discodorididae Bergh, 1891

Genus *Anisodoris* Bergh, 1898

Anisodoris fontaini (d’Orbigny, 1837)

(Figure 2)

“Doris”, “Island of Caylen” (Queilén on Chiloé Island or Cailin Island, near Chiloé?), December 1834, “common under large stones”, CD Page 284, Species No. 1091.

REMARKS

The “Doris” from Caylen differs from *Anisodoris punctuolata* (d’Orbigny, 1837) in its “egg-yellow” colouration and having “rounded” tubercles “of two sizes”. In fact, there is only a single large, yellow Magellanic dorid species with two-sized, rounded tubercles, the common *A. fontaini*. All the externally similar species, *Anisodoris tessellata* Bergh, 1898, *Neodoris carvi* Marcus, 1959, *Neodoris erinacea* Marcus, 1959, and *Archidoris incerta* Bergh, 1898, were shown to be junior synonyms of *A. fontaini* recently (MUNIAÍN *et al.*, 1991; SCHRÖDL, 1997c, 2000a).

Anisodoris punctuolata (d’Orbigny, 1837)

(Figure 3)

“Doris”, East Falkland Islands, 7 March 1833, 7 specimens, body dimensions 8.3 cm length: 3.8 cm width, CD Page 151.

REMARKS

This flattened, oval-shaped dorid with broad mantle externally resembles a group of similar, uniformly white or yellowish cryptobranch doridoideans, i.e. *Gargamella immaculata* Bergh, 1894, *Austrodoris kerguelenensis* (Bergh, 1884) and *Anisodoris punctuolata*. Only the latter two species reach the large body size of “3 1/4 inches” mentioned by DARWIN. Dense, minute notal tubercles (“surface... thickly studded with minute cylindrical papillae”) only occur in *A. punctuolata*. Very interesting are DARWIN’s detailed observations on the spawn (CD Page 151) describing egg-ribbons up to 20 inches long with no less than 600 000 eggs. Spawn of most Magellanic nudibranch species was studied by the author (unpublished data): only one large-sized, uniformly white or yellowish coloured Magellanic species with minute tubercles has been observed to produce such an enormous egg-ribbon, the common *Anisodoris punctuolata* (d’Orbigny, 1837).

?Discodorididae sp.

“Doris” (larger species), Cerro Tres Montes, Chonos Archipelago, December 1834, at 4 m depth, CD Page 292, Species No. 1108.

REMARKS

DARWIN (p. 292) suspected the “larger” (no dimension)



dorid being “pale yellow, with irregular brown spots” to be conspecific with the “Doris” (= *A. punctulata*) from East Falkland Islands. Since no body dimensions are given, *Diaulula hispida* (d’Orbigny, 1837) (see SCHRÖDL, 2000b) could have been meant as well: its characteristic undulating ridge on the notum may be poorly developed and difficult to detect in individuals smaller than 3–4 cm (own observations).

?Platydorididae Bergh, 1891

cf. *Gargamella immaculata* Bergh, 1894

“Doris” (smaller species), Cerro Tres Montes, Chonos Archipelago, December 1834, at 4 m depth, 1.8 cm body length, CD Page 292, Species No. 1108.

REMARKS

The “smaller, bright yellow” specimen from C. Tres Montes might be *Gargamella immaculata* Bergh, 1894 (see SCHRÖDL, 1996, 1997a) having uniform colouration and “ten, small, delicate, brush-like” gills, but the description is too incomplete to be sure.

Doridoidea: Phanerobranchia: Polyceridae Alder & Hancock, 1845

Genus *Thecacera* Fleming, 1828

Thecacera darwini Pruvot-Fol, 1950

(Figures 4,5)

“Nudibranch”, Cerro Tres Montes, Chonos Archipelago, December 1834, at 4 m depth, body length 2.5 cm when “extended”, CD Pages 291–292, pl. 16, fig.1; Species No. 1106.

REMARKS

This “nudibranch” from C. Tres Montes was exceptionally well characterized by DARWIN’s external description: “...body very narrow, mantle not surpassing the foot, tail very much and abruptly pointed,....No labial (oral) tentacula, ...antennae (rhinophores) at their bases are enclosed in a case; which on the 2/3 of its exterior margin expands out into a saucer (rhinophoral sheath), the edges of which are intended with about 8 points, ...the branchiae are seated in very middle of the back; consist of five trees...placed in circle...A little posteriorly to the branchiae and a little exteriorly to them, there are two cylindrical, obtusely ended, tentacula-like organs rather longer than branchiae... Body white, singularly transparent: scattered over whole surface there are circular and oblong regular marks...color dark brown... The saucer-like case of tentacula: the branchiae, excepting the very tips: and central broad band in the two posterior cylindrical organs (top and base white): and narrow margin at very extremity of tail, bright orange. Hence very pretty animal”. An interesting morphological detail is indicated in plate 16, fig. 1 (see Fig. 5): both the distal portions of male and female genital ducts are everted in dead speci-

mens. These genital ducts are also everted by living specimens ready for copulation (own observation). In aquaria, *T. darwini* is able to float upside down on the water surface, confirming DARWIN’s observation. In contrast to DARWIN’s assumption “can probably swim well”, *T. darwini* has never been observed swimming in natural surrounding or in laboratory. DARWIN correctly recognized this polycerid species as being “allied, especially in habits, to the molluscous one (hereby being identified as *Polycera* sp.) of Rio (CD p. 46). There can be no more doubt that DARWIN’s Chilean polycerid specimens belong to *Thecacera darwini* Pruvot-Fol, 1950, which was described from preserved material from the Musée Nationale d’Histoire Naturelle Paris without knowing DARWIN’s description in detail. Other polycerids from Magellanic waters, *Polycera marplatensis* Franceschi, 1928, and *P. priva* Marcus, 1959, clearly differ in colouration and body shape (for redescriptions see SCHRÖDL, 1996; MUNIÁIN & ORTEA, 1998).

Aeolidoidea

Facelinidae Bergh, 1890

Genus *Phidiana* Gray, 1850

Phidiana lottini (Lesson, 1831)

(Figure 6)

“Cavolina”, Chiloé, December 1834, “under stones”, 3.8 cm body length (crawling), CD Page 257, Species No. 1091.

REMARKS

The “Cavolina” from Caylen (CD p. 284) is not a pteropod Thecosomata as suggested by its misleading name, but an aeolidoidean nudibranch. The “general color crimson & brownish purple R. Mouth and under side finer rose color. Branchiae (cerata) composed of conical fillets, basal parts leaden colored, arranged in numerous transverse rows on each side of back...Anterior and inferior tentacula (oral tentacles) placed far apart..., very long, tapering, pointed, tipped with white” allow little doubt that DARWIN found *Phidiana lottini* (Lesson, 1831). This species is common along the coasts of southern Chile to Peru and was previously known under its junior synonym *Phidiana inca* (d’Orbigny, 1837). DARWIN also described the rhinophores as the “posterior and superior tentacula” being “blunt and much shorter, placed between (the latter word crossed out) behind some of the first rows of branchiae”, while beginning not anterior to the level of the rhinophores in *P. lottini*. However, *Aeolidia papillosa* var. *serotina* Bergh, 1873, the only southern Chilean species with ceratal rows beginning anterior of the rhinophores, clearly differs in colouration, so that DARWIN’s first observation that the rhinophores are “placed between” the first cerata appears to be correct.

DISCUSSION

In summary, DARWIN collected one notaspidean, at least four (probably six) different nudibranch species, and a dubi-



ous opisthobranch species from Magellanic waters but no museum material remains. More than 175 years after the "Beagle" cruise, however, every current researcher must be astonished at the detailed examination and description of some of his specimens, although without establishing and naming new species. He combined morphological and biological information which, in the case of *Anisodoris punctuolata*, now enabled species identification. DARWIN even dissected specimens of *A. punctuolata*, thus providing some anatomical information, long time before other researchers recognized the importance of anatomical studies in opisthobranchs; all this in the consideration that DARWIN was not a molluscan specialist and only had rudimentary literature at his disposal (see KEYNES, 1997). The most striking example for DARWIN's accuracy is his detailed and unambiguous morphological and biological description of *Thecacera darwini*. This beautiful nudibranch species was named in DARWIN's honour by PRUVOT-FOL (1950), however, without knowing his early description in detail. With the present study, *T. darwini* is confirmed as definitely referring to DARWIN's species.

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